

## Hardness as a Basis of Fruit Choice in Two Sympatric Primates

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**ABSTRACT** Fruit color and size are significant determinants of food choice in mammals and birds, but hardness, an important physical property of fruit and seeds, has generally been overlooked as a determinant of food choice in studies of mammalian foraging behavior. Two methods were used to determine fruit hardness during a field study of two sympatric primates, the black spider monkey (*Ateles paniscus*) and the bearded saki monkey (*Chiropotes satanas*) in Surinam. We measured both puncture resistance of fruit pericarp and crushing resistance of seeds. Puncture resistance of the pericarp of some fruit opened by *Chiropotes* was as much as 15 times greater than that of all fruit successfully opened by *Ateles*. In contrast, crushing resistance of species of seeds masticated by *Chiropotes* was significantly lower than that of seeds swallowed by *Ateles*. These data demonstrate that hardness of both fruit pericarp and seed may play a significant role in food choice among sympatric vertebrates. Measurements of both puncture resistance of the pericarp and crushing resistance of the seed are necessary for understanding the significance of fruit hardness in these primates.

In tropical forests most of the vertebrate biomass is supported by fruit resources (Fleming et al., 1987). Frugivores suffer from the disadvantage that the distribution of their feeding sources is usually patchy in both time and space (e.g., Oates, 1986; Fleming et al., 1987; Dunbar, 1988). Any adaptation that increases the probability of obtaining such patchy resources will have selective value. Seeds of fruit are a particularly valuable part of the fruit resource, since they contain relatively high concentrations of protein and fat and (at early stages of ripeness in some fruit) tend to have low concentrations of toxic compounds (Ayres, 1986). Plants therefore protect such resources with thick endocarps or other coverings until the kernels are either sufficiently developed to be dispersed and/or toxic compounds have been added for their protection. A frugivore that can penetrate these protective coverings has preferential access to the resource, but mammals attempting to eat unripe fruit face both metabolic and mechanical problems. In this study we confront the major

mechanical problem—hardness of the fruit's exterior covering.

### FOOD CHOICE

In contrast to numerous studies of food selection in folivorous primates (Gautier-Hion and Gautier, 1974; Struhsaker, 1975, 1978; McKey, 1978; McKey et al., 1981; Milton, 1979, 1981; Oates et al., 1980; Waterman and Choo, 1981; Baranga, 1982; Glander, 1982), food selection by frugivorous primates has received less attention. Color and size have been found to be significant determinants of fruit choice in mammals and birds (Turcek, 1963; Snodderly, 1979; Janson, 1983; Gautier-Hion et al., 1985; Wheelwright, 1985; Fleming et al., 1987). Both physical and chemical changes in fruit during ripening (e.g., increased palatability,

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change in color, reduction of pericarp toughness) probably contribute to the attractiveness of ripe fruit for primates.

Field studies of frugivores have not usually compared the percentages of ripe and unripe fruit in the diet (a significant exception is Foster 1977). It appears that relatively few primates, except those that also eat leaves, regularly choose unripe over ripe fruit (*Hylobates syndactylus* [Chivers, 1974], *Presbytis senex* [Hladik, 1977], *P. obscura* [Curtin, 1980] or consume substantial quantities of unripe fruit at certain times of the year (*Colobus guereza* [Oates, 1977], *Alouatta palliata* [Milton, 1980], *Presbytis rubicunda* [Davies, 1984]). A major exception is the tribe (Rosenberger, 1988) of frugivorous New World Pitheciini (*Cacajao*, *Chiropotes*, *Pithecia*) [Buchanan et al., 1981; Ayres, 1986; van Roosmalen et al., 1988; Robinson et al., 1987].

#### PREVIOUS STUDIES OF FRUIT HARDNESS

Although some authors have recognized the potential value of using physical characteristics of fruit to document differences in food choice (e.g., Cant and Temerin, 1984; Chivers et al., 1984), hardness has rarely been quantified. For example, Waser (1987:224) proposed that "larger heavier-jawed" primate species eat "thicker, tougher fruits." In support of this presumed trend, Terborgh (1983) showed that larger, stronger *Cebus apella* were able to gain access to the seeds of *Astrocaryum* nuts at a faster rate than smaller, sympatric *C. albifrons*. Gautier-Hion et al. (1985) investigated several characteristics of fruit, including seed protection, in their extensive study of fruit choice in West African birds and mammals, but they did not specifically measure fruit hardness. Ayres (1986) found that *Cacajao* preferred seeds from fruit with hard husks; he divided fruit qualitatively into those whose husks were either soft, medium, or hard.

While puncture resistance has received little attention, there has been interest in measuring crushing resistance of fruit eaten by domestic turkeys (Schorger, 1960), Central American mammals (Janzen and Higgins, 1979), bats (August, 1981), peccaries (Kiltie, 1982; Smythe, 1986), and cebus monkeys (Kiltie, 1982). Peters and Maguire (1981) and Peters (1987) measured the compressive force required to fracture African plant foods eaten by humans, chimpanzees, mangabeys, baboons, and a variety of other

mammals; Boesch and Boesch (1983) tested five of these species eaten by chimpanzees. All of these studies measured crushing resistance (except that of the Boesch's, which measured resistance to impact), and, with the exception of August (1981), all measurements were obtained in the laboratory and without consideration for possible changed properties of fruit in the dried state.

#### DENTAL CRITERIA AND FRUIT HARDNESS

Previous studies did not measure resistance to puncturing. For many heterodonts ingestion requires at least two distinct abilities: to open (puncture) a food resource and to masticate it (if the food is masticated before swallowing). Frequently the anterior dentition is used for puncturing and the posterior dentition for crushing. For such animals, methods to date lack the ability to assess the importance of hardness as a determinant of fruit choice, because no distinction was made between puncturing and crushing.

It is well known that physical properties of food have a selective influence on features of the teeth in mammals (Kay, 1973; Rosenberger, 1973; Rosenberger and Kinzey, 1976; Kay and Hylander, 1978; Kinzey, 1978; Seligsohn and Szalay, 1978; Smith, 1983; Grine, 1984; Herring, 1985; Lucas and Luke, 1985). Thus features of canine teeth allow animals to exploit foods with differing resistances to puncturing, and features of molars allow animals to exploit foods with differing resistances to crushing. In the case of peccaries (Kiltie, 1982), whole fruits are crushed by molars; in the case of bearded sakis in this study, fruits may be opened (punctured) by canines to obtain seeds that are masticated (crushed) by molars.

The pitheciin primates (*Chiropotes*, *Cacajao*, and *Pithecia*) all have quadritubercular molars with very low relief, unique canines that are very robust, laterally divergent, and widely separated from neighboring upper and lower incisors, and lower incisors that are laterally compressed into a robust, procumbent gouge (HersHKovitz, 1985). We chose to investigate the role of fruit hardness in the diet of one such pitheciin, *Chiropotes satanas*, and we collected similar data on a sympatric frugivore, *Ateles paniscus*. The molars of *Ateles*, unlike those of *Chiropotes*, are clearly those of a typical frugivore (Kay, 1973). The molars of *Ateles* show higher relief than those of *Chiropotes*, and the canines are neither laterally divergent nor as robust as those of *Chiropotes*. The canines of *Chiro-*



*potes* are particularly well suited to opening fruit with high resistance to puncturing, and the molars are well suited to the crushing of seeds. The virtual lack of sexual dimorphism in dental morphology of both species (Swindler, 1976; Hershkovitz, 1985) suggests that their unique dental features are related to feeding and not to social behavior.

#### MATERIALS AND METHODS

##### *Study site and study animals*

This study was conducted as part of a long-term project in Raleighvallen-Voltzberg Nature Reserve in central Surinam (4°41'N, 56°10'W) (Kinzey, 1987). Mittermeier and van Roosmalen (1981) provide a complete description of the study site. We studied a troop of 16 bearded saki monkeys (*Chiropotes satanas chiropotes*) and a troop of 12 black spider monkeys (*Ateles paniscus paniscus*). *Chiropotes* and *Ateles* spend virtually all their time in two of the five forest types available: high forest and mountain savanna forest. Bearded sakis average about 3 kg body weight, with little sexual dimorphism (Mittermeier, 1977; Ayres, 1981), and spider monkey males average 7.9 kg, with females slightly smaller (7.7 kg; Mittermeier, 1977). The data reported here were obtained during September 1986 through February 1987—the long dry season through the short wet season.

##### *Sampling methods and equipment*

We timed the duration of feeding minutes in each feeding tree (from first animal into the tree to last animal leaving, unweighted for number of animals in the tree) for a total of 2,086 feeding minutes for *Chiropotes* and 3,539 feeding minutes for *Ateles*. We recognize that this method overlooks feeding durations of individuals, but it provides an estimate of relative importance of various fruit species in the diet for each troop. *Chiropotes* traveled long distances each day, rapidly moving from feeding tree to feeding tree. The troop commonly divided into subgroups, usually remaining in vocal communication while feeding, but it was difficult for a single observer to keep the entire troop within visual range. Hence, total feeding minutes was an underestimate for the sakis, although we attempted to identify all of the feeding trees used each day. *Ateles* also divided into subgroups, but ranging patterns among subgroups were seldom coordinated. We followed a single subgroup, documenting fission and fusion, throughout the day. *Ateles*

was more accustomed to the presence of observers than was *Chiropotes*, but all day tracking was possible for both species, 134 hours for *Chiropotes* and 242 hours for *Ateles*.

A monkey rarely consumes entire fruit; we gathered pieces of fruit dropped by the monkeys and immediately determined how much of the fruit had been eaten. We also gathered each whole fruit dropped and determined whether an unsuccessful attempt had been made to open it. Same day measurements of fruit hardness of dropped fruit (including partially eaten and uneaten fruit) were taken using simple portable instruments: an agricultural fruit tester (Fruit & Vegetable Tester, Model 719-40MRP, John Chatillon & Sons, Inc., Kew Gardens, NY), which measures resistance to puncturing, and a soil compression tester ("Rimac Spring Tester," Rinck-McIlwaine, Inc., Dumont, NJ), which measures resistance to crushing forces up to 160 kg (Fig. 1).

Food processing includes puncturing, cutting, and shearing, which involve high occlusal pressure, and crushing and grinding, which involve relatively low occlusal pressure. These terms have been defined by Rosenberger and Kinzey (1976). We have chosen to measure puncturing and crushing which have different mechanical effects upon food. These terms are not to be confused with the term *puncture-crushing*, used to describe a type of masticatory cycle (e.g., Hiiemae and Kay, 1972).

The fruit tester was equipped with a pin vise holding a round plunger, 1.6 mm (1/16 inch) in diameter, and measured forces up to 18 kg, which translated to pressures up to 9.1 kg/mm<sup>2</sup>. To determine pressures in excess of 9 kg/mm<sup>2</sup>, a similar 1/16 inch diameter plunger was fitted to the soil compression tester. It is important for standardized comparisons that the same sized plunger be used for all measurements of resistance to puncturing.<sup>1</sup> Measurements were obtained by slowly pushing the plunger at a constant rate into the fruit or fruit fragment. The maximum force applied immediately prior to puncture of the edible part was recorded by the maximum reading device. If the edible part was mesocarp, measurements assessed the resistance of exocarp. If the edible part was the seed, measurements assessed the

<sup>1</sup>Because of the current unavailability of the fruit tester, an alternative is a force gage model FDL, available from Wagner Instruments, P.O. Box 1217, Greenwich, CT 06836. In either case, a 1/16 inch diameter plunger must be fitted to the instrument.



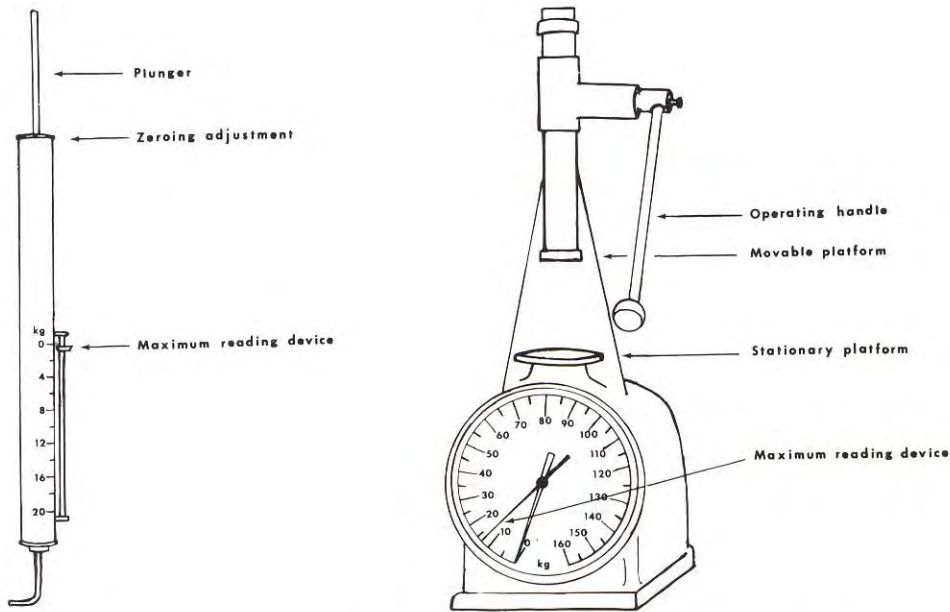


Fig. 1. Left: Puncture device: agricultural fruit tester. Right: Crushing device: soil compression tester. See text for description of instruments.

resistance of the entire pericarp, including the endocarp. Each fruit, or fruit fragment, was tested three times with the fruit tester, and the three measurements were averaged. Preliminary tests at the onset of the study showed that measurements of fruit fragments were representative of the whole fruit. The size of the fragment did not influence measurement of puncture resistance.

Measurements of maximum resistance of seeds to compression were taken with the compression tester. Measurements were obtained by slowly compressing each seed until it collapsed, and the maximum compressive force was recorded. Peters and Maguire (1981) previously determined that there was no systematic relationship between speed of loading and the force at which fracture occurred. Since an object is destroyed in the process of measuring its resistance to compression, only one compression measurement was taken on each seed. Crushing forces could not be translated to pressures because of the changing surface area of the seed as it deformed during its resistance to crushing. Only whole seeds were subjected to compression testing. To obtain crushing data on species of fruit eaten by *Ateles*, measurements were obtained from whole seeds

that had passed through the intestinal tract and from seeds discarded in partially eaten fruit. For any given species of fruit there was no difference in resistance between seeds obtained from these two sources ( $P > 0.20$ , two-tailed *t* tests), so the data were combined. Since *Chiropotes* masticates most seeds, whole seeds were less readily obtainable. No whole seeds were found in the feces. To obtain crushing data on species of fruit eaten by *Chiropotes*, whole seeds were obtained from fruit partially eaten by *Chiropotes* and dropped to the ground. We assume these seeds to be representative of those eaten, since the husks dropped did not contain unusually hard or unusually soft seeds. Using these two methods, we were able to distinguish between puncture resistance (which measures the maximum pressure required to open the fruit) and crushing resistance (which measures the maximum bite force required to masticate the seed).

## RESULTS

### *Interspecific dietary differences*

Fruit represented over 90% of the timed samples of both *Ateles* and *Chiropotes* (Table 1), but there were significant differences in the parts of the fruit that were eaten



TABLE 1. Dietary overlap between *Chiropotes satanas* and *Ateles paniscus* in Surinam

Component of diet	Percent time feeding	
	<i>C. satanas</i> (n = 2,141 feeding minutes)	<i>A. paniscus</i> (n = 3,520 feeding minutes)
Total fruit	97.1	93.1
Seeds with aril <sup>1</sup>	4.3	69.6
Seeds only	86.4	0
Aril only	5.6	9.2
Exocarp only	0	0.3
Whole fruit	0.8	14.0
Young leaves	1.4	3.0
Flowers	1.0	2.9
Bark	0.5	1.0
Total	100.0	100.0

<sup>1</sup>*Chiropotes* masticated seeds with aril; *Ateles* swallowed seeds whole with aril.

( $P < 0.001$ ,  $\chi^2$ ). *Ateles* either swallowed fruit whole (when the exocarp was thin and the fruit small) or removed the exocarp with the teeth and swallowed the seed along with the aril. Very large seeds (e.g., *Catostema fragrans*) were spit out. van Roosmalen (1984) suggested that mild detergent action by the digestive tract only removes adherent testa without destroying the seed during digestion, and our observations of whole voided seeds confirmed this. *Chiropotes* masticated seeds, discarding the pericarp, and occasionally consumed arils with the seeds. Both primates devoted proportionately little time to eating leaves, flowers, or bark. We did not observe either monkey to eat invertebrates.

#### Fruit hardness: Puncture resistance of the pericarp

Puncture resistance was quantified for 132 specimens from 26 species of fruit eaten by *Ateles* and for 231 specimens from 34 species of fruit eaten by *Chiropotes*. The maximum resistance value for the exocarp of all indehiscent fruit eaten by *Ateles* was 1.18 kg/mm<sup>2</sup> (*Priourella* sp.; Table 2). Spider monkeys discarded fruit of *Guettarda acreana* and *Rheedia macrophylla* after briefly attempting to bite into them when puncture resistance was greater than 1.25 kg/mm<sup>2</sup>. In the case of *Priourella* sp., *Ateles* attempted to eat both yellow and green fruit so they were not selecting solely on the basis of color of fruit that was yellow when ripe and green when unripe. Rather, they discarded all specimens (except one) of *Priourella* when puncture resistance was greater than 1.17 kg/mm<sup>2</sup> (Table 3). It is possible that juvenile and female animals were less able to puncture the harder fruit.

Dehiscent fruit such as *Swartzia*, *Tetragastris*, and *Virola* were eaten by *Ateles* when ripe. Partially open valves of these fruit improved access by enabling the spider monkeys to pry open the fruit with their incisors or with their fingers. For dehiscent fruit, therefore, our measures of puncture resistance may have overestimated the degree of mechanical difficulty involved in opening them.

Many fruit eaten by bearded saki monkeys were harder than those eaten by spider monkeys (Table 2). Puncture resistance values of the pericarp of fruit eaten by *Chiropotes* ranged from 0.025 kg/mm<sup>2</sup> (*Clarisia racemosa* and *Ecclinusa guianensis*) to 37.8 kg/mm<sup>2</sup> (*Licania majuscula*). The average puncture resistance of fruit eaten by *Chiropotes* (2.77 kg/mm<sup>2</sup>) was significantly greater than that of fruit eaten by *Ateles* (0.03 kg/mm<sup>2</sup>;  $P < 0.0001$ , Mann-Whitney U test).

Eleven of the 49 fruit species listed in Table 2 were shared by *Ateles* and *Chiropotes*. In three cases (*Brosimum lactescens*, *Clarisia racemosa*, and *Drypetes variabilis*) in which puncture resistance was low, *Ateles* and *Chiropotes* both fed on the fruit when it was ripe. For the other cases, there was variable time lag between the first date when *Chiropotes* ate the fruit and the first date the fruit was eaten by *Ateles* (Table 4). A comparison of puncture resistance values suggests that *Ateles* fed on these fruit only after they had softened and/or ripened. In the cases of *Couratari stellata*, *Lecythis corugata*, *Naucleopsis guianensis*, *Priourella* sp., and *Swartzia benthamiana*, *Chiropotes* opened the fruit to extract the seeds before the fruit was ripe and when puncture resistance was as high as 7.33 kg/mm<sup>2</sup> (in the case of *Couratari stellata*). These species were also eaten by *Ateles*, but only when they were softer (maximum puncture resistance, 1.18 kg/mm<sup>2</sup>).

Both *Ateles* and *Chiropotes* ate parts of *Licania majuscula* fruit. When it was ripe *Ateles* used incisors to scrape the thin mesocarp (puncture resistance, 0.025 kg/mm<sup>2</sup>) from the bony endocarp. The puncture resistance of the entire pericarp (essentially the resistance of the endocarp) at this stage was as low as 1.47 kg/mm<sup>2</sup>, still too high for *Ateles* to penetrate the endocarp. In the unripe stage, as well as when ripe, *Chiropotes* punctured the entire pericarp (including the endocarp) with their canines and was able to gain access to the protein-rich kernel inside.



TABLE 2. Puncture resistance of fruit species eaten by *Chiropotes satanas* and *Ateles paniscus* in Surinam<sup>1</sup>

Species of fruit	<i>Chiropotes</i> (kg/mm <sup>2</sup> )					<i>Ateles</i> (kg/mm <sup>2</sup> )				
	No.	Min.	Mean	S.D.	Max.	No.	Min.	Mean	S.D.	Max.
<i>Achrouteria pomifera</i>	26	1.43	2.29	0.43	3.3					
<i>Anomoctenium granulosum</i>	1	10.2	—		10.2					
<i>Aspidosperma excelsum</i>						1	0.79	—		0.79
<i>Bagassa guianensis</i>						4	0.03	0.15	0.10	0.27
<i>Brosimum lactescens</i>	5	0.17	0.21	0.03	0.24	20	0.03	0.3	0.20	0.88
<i>Brosimum parinarioides</i>	3	0.37	0.47	0.14	0.62					
<i>Carapa procera</i>	9	0.72	0.89	0.15	1.08					
<i>Catostemma fragrans</i>						5	0.46	0.58	0.17	0.88
<i>Cedrela odorata</i> <sup>2</sup>	3	2.07	2.65	0.54	3.13					
<i>Clarisia racemosa</i>	1	0.03	—		0.03	1	0.03	—		0.03
<i>Cordia sericicalyx</i>						3	0.13	0.14	0.004	0.14
<i>Couratari stellata</i>	15	1	3	1.87	7.33	1	0.79	—		0.79
<i>Drypetes variabilis</i>	2	0.05	0.07		0.08	1	0.76	—		0.76
<i>Ecclinusa guianensis</i>	21	0.03	0.31	0.18	0.62					
<i>Eperua falcata</i>	1	6.06	—		6.06					
<i>Eremoluma sagotiana</i>	22	0.37	0.59	0.18	0.81	3	0.1	0.21	0.10	0.29
<i>Guarea grandifolia</i>	1	1.79	—		1.79					
<i>Guettarda acreana</i>						1	0.69	—		0.69
<i>Inga acrocephala</i>	2	0.89	0.99		1.08					
<i>Inga alba</i>						4	0.39	0.58	0.26	0.97
<i>Inga borgoni</i>	1	1.2	—		1.2					
<i>Inga cinnamonea</i>	4	2.44	3.13	1.22	4.97					
<i>Lecythis chartaceae</i> <sup>3</sup>	5	0.65	0.9	0.19	1.11					
<i>Lecythis corrugata</i> <sup>3</sup>	20	0.44	1.06	0.58	2.19	8	0.58	0.7	0.12	0.95
<i>Licania apetala</i>	10	2.98	3.83	0.71	4.8					
<i>Licania majuscula</i>	18	1.47	18.07	9.37	37.8	1	0.03	—		0.03
<i>Moutabea guianensis</i>	12	0.32	0.88	0.43	1.62					
<i>Naucleopsis guianensis</i>	5	0.57	1.45	0.52	1.84	3	0.03	0.09	0.06	0.15
<i>Parinari excelsa</i>						8	0.13	0.25	0.12	0.52
<i>Paullinia spicata</i>	6	0.66	0.72	0.06	0.8					
<i>Potamogonos microcalyx</i>	3	2.99	4.03	1.21	5.37					
<i>Pourouma guianensis</i>						3	0.47	0.6	0.14	0.74
<i>Priourella</i> sp.	4	1.37	1.43	0.06	1.5	16	0.45	0.81	0.17	1.18
<i>Protium polybotryum</i>						4	0.13	0.3	0.16	0.49
<i>Qualea dinizii</i>	2	2.45	2.57		2.68					
<i>Quassia simarouba</i>	8	0.4	0.92	0.23	1.11					
<i>Rhedia macrophylla</i>						4	0.67	0.68	0.02	0.72
<i>Sacoglottis cydonioides</i>						1	0.63	—		0.63
<i>Strychnos tomentosa</i>						8	0.47	0.73	0.13	0.92
<i>Swartzia benthamiana</i> <sup>2</sup>	3	1.2	1.22	0.01	1.23	2	0.83	0.97		1.09
<i>Swartzia schomburgkii</i> <sup>2</sup>	2	1.36	1.98		2.6	6	1.14	1.25	0.11	1.4
<i>Tanaecium nocturnum</i>	3	1.34	1.51	0.15	1.63					
<i>Tetragastris altissima</i> <sup>2</sup>						3	0.18	0.38	0.20	0.58
<i>Tetragastris panamensis</i> <sup>2</sup>	3	0.53	0.83	.35	1.21					
<i>Virola melinonii</i> <sup>2</sup>						15	0.75	0.88	0.11	1.11
<i>Virola surinamensis</i> <sup>2</sup>						6	0.53	0.7	0.11	0.84
Liana No. 1	6	0.72	0.93	0.26	1.38					
Liana No. 2	2	0.32	0.43		0.54					
Apocynaceae, sp. unknown	2	0.77	0.91		1.04					
Total range	231	0.03	2.77		37.8	132	0.03	0.58		1.4

<sup>1</sup>N = sample size. Min. and Max. are minimum and maximum recorded average pressures of resistance to puncturing. All fruit taxa are according to van Roosmalen (1985) except when indicated otherwise.

<sup>2</sup>Fruit that are dehiscent.

<sup>3</sup>Fruit taxa according to Mori and Prance (1989).

Thus, using different processing techniques, the two primates consumed different parts of the same species of fruit, each part with a different degree of hardness—*Ateles* only the soft mesocarp and *Chiropotes* only the seed, covered by its hard endocarp.

#### Fruit hardness: Crushing resistance of seeds

Crushing resistance was quantified for 151 seeds from 13 species of fruit eaten by *Ateles* and from 19 species of fruit eaten by



TABLE 3. Puncture resistance of individual fruit of *Priourella* sp. (Sapotaceae) partially eaten or dropped uneaten by *Ateles paniscus*

Specimen No.	Animal <sup>1</sup>	Result	Resistance <sup>2</sup>
210	?	Not eaten	1.79 ± 0.07
205	?	Not eaten	1.56 ± 0.05
204	?	Not eaten	1.55 ± 0.13
201	?	Not eaten	1.37 ± 0.03
200	F	Not eaten	1.37 ± 0.03
199	Male	Not eaten	1.35 ± 0.02
198	F	Not eaten	1.33 ± 0.07
197	Male	Not eaten	1.33 ± 0.02
196	Male	Not eaten	1.30 ± 0.07
195	?	Not eaten	1.26 ± 0.06
194	Male	Not eaten	1.25 ± 0.05
101	Male	Eaten	1.18 ± 0.03
190	F or J	Not eaten	1.17 ± 0.05
100	Male	Eaten	1.09 ± 0.08
099	Male	Eaten	1.00 ± 0.03
098	Male	Eaten	0.87 ± 0.05
097	Male	Eaten	0.87 ± 0.03
096	J	Eaten	0.83 ± 0.11
095	Male	Eaten	0.82 ± 0.03
094	J	Eaten	0.78 ± 0.13
093	F	Eaten	0.77 ± 0.05
092	F	Eaten	0.76 ± 0.03
091	F	Eaten	0.74 ± 0.03
090	F	Eaten	0.74 ± 0.08
089	F	Eaten	0.69 ± 0.02
088	Male	Eaten	0.68 ± 0.08
087	J	Eaten	0.65 ± 0.04
086	J	Eaten	0.45 ± 0.02

<sup>1</sup>F, female; J, juvenile.

<sup>2</sup>Mean ± S.E. Ranked in order of decreasing hardness.

*Chiropotes* (Table 5). The average crushing resistance of seeds of fruit eaten by *Chiropotes* ( $7.2 \pm 0.66$  kg) was significantly less than that of seeds of fruit swallowed whole by *Ateles* ( $17.1 \pm 2.64$  kg) ( $P < 0.0001$ , Mann-Whitney U test). None of the seeds swallowed by *Ateles* was observed to have been chewed, and we found both large and small whole seeds in *Ateles* feces. In contrast, no whole seeds were found in *Chiropotes* feces. *Chiropotes* chewed primarily soft seeds—soft enough to be thoroughly masticated.

#### DISCUSSION

Throughout most of the Guianas *Chiropotes* and *Ateles* are sympatric. They overlap in habitat preference, height of forest canopy used for feeding, and species of fruit eaten (Mittermeier, 1977; Mittermeier and van Roosmalen, 1981). We investigated fruit hardness as a basis for fruit choice in these two sympatric frugivores. *Ateles* preferred ripe fruit and dispersed most seeds; *Chiropotes* consumed a significant portion of unripe fruit and consumed most seeds.

We quantified the degree of hardness of both the exocarp of fruit opened by *Chiropotes* and the seeds consumed by them. *Chiropotes* is known to eat 34 species of fruit also eaten by *Ateles*, but at earlier stages of ripeness (van Roosmalen et al., 1988). For five of these fruit species, we documented quantitatively the degree of hardness (ripeness) above which the puncture resistance was presumably too great for *Ateles* to open. In addition, we found that *Chiropotes* was capable of opening at least 15 species of fruit whose exocarps were presumably too hard for *Ateles* to open. Ten of these species are fruit known to be eaten by *Ateles* (van Roosmalen, 1980; Kinzey and Norconk, personal observation), presumably at more advanced stages of ripeness. *Chiropotes* could have opened any of the fruit discarded by *Ateles* in this study and frequently did eat fruit within the range of hardness values of fruit eaten by *Ateles*. Despite its capability to open fruit with tough husks, *Chiropotes* apparently also has an upper limit to this capability. Most specimens of *Licania majuscula* with resistances above  $32 \text{ kg/mm}^2$  were dropped unopened, although they frequently had been scratched by canine teeth.

Although there is dietary overlap, we have demonstrated two ways in which the bearded saki is able to obtain hard food resources that are unavailable to the spider monkey. In the case of fruit like *Couratari stellata*, *Chiropotes* fed at an earlier (harder)

TABLE 4. Comparison of times of initial fruit selection for *Chiropotes* and *Ateles*<sup>1</sup>

Species of fruit	First date fruit was eaten	
	<i>Chiropotes</i>	<i>Ateles</i>
<i>Priourella</i> sp.	9/24/86	10/11/86
<i>Licania majuscula</i>	10/29/86	11/12/86
<i>Couratari stellata</i>	11/02/86	1/21/87
<i>Inga alba</i>	11/02/86	11/11/86
<i>Clarisia racemosa</i>	12/04/86	12/11/86
<i>Swartzia benthamiana</i>	1/04/87	1/08/87
<i>Brosimum lactescens</i>	1/10/87	12/06/86
<i>Naucleopsis guianensis</i>	1/10/87	1/17/87
<i>Lecythis corrugata</i>	1/10/87	2/17/87
<i>Eremoluma sagotiana</i>	1/14/87	2/13/87
<i>Drypetes variabilis</i>	2/22/87	12/26/86

<sup>1</sup>In the majority of cases (*Priourella* sp., *Licania majuscula*, *Couratari stellata*, *Swartzia benthamiana*, *Naucleopsis guianensis*, and *Eremoluma sagotiana*) *Ateles* ate these fruit only when puncture resistance was less than the minimum resistance of the same species eaten by *Chiropotes*. In the case of *Inga alba* we did not obtain puncture data for *Chiropotes*. Only in the cases of *Brosimum lactescens* and *Drypetes variabilis*, in which *Chiropotes* ate the fruit at very low levels of puncture resistance, did the date of initial fruit selection by *Ateles* precede that of *Chiropotes*.



stage of ripeness; in the case of fruit like *Licania majuscula*, *Ateles* fed only on the soft mesocarp while *Chiropotes*, often feeding at the same stage of ripeness, used their canines to open the hard 0.5 cm thick endocarp to obtain the seed inside. Thus *Chiropotes* is able to rob unripe fruit from the tree, but may be encountering more toxins than *Ateles* in the process.

Kay (1988) demonstrated a marked difference between the microwear patterns of teeth of *Chiropotes* and *Ateles*. He suggested that microscopic pits on lower molars of *Chiropotes* and scratches on the homologous molars of *Ateles* should correlate with a diet of hard food items in the former and soft fruit in the latter. Our field study confirms his observations.

In a recent study of *Cacajao calvus calvus*, Ayres (1986) provides nutritional and chemical evidence for fruit selection in the pithe-

ciins. Fruit pericarp hardness was positively correlated with fat content of the seed. He found fat content to be associated with protein content, although there was no significant difference between the protein content of seeds from ripe and unripe fruit. Condensed tannins were present, but were quantitatively less in the seeds of unripe fruit, and the overall nutritional value of unripe seeds was significantly higher than seeds of the same species of ripe fruit. We found an inverse relationship between hardness of the pericarp and hardness of the seed. If resistance to crushing reflected the density of the seed testa, *Chiropotes* could be avoiding seeds that were potentially toxic or difficult to digest. Seed hardness was not a significant deterrent to *Ateles*, since they neither chewed most seeds nor digested them.

Although the seed embryo may exhibit less chemical defense than leaves of the same

TABLE 5. Crushing resistance of whole seeds of species of fruit swallowed by *Ateles paniscus* and masticated by *Chiropotes satanas* in Surinam

Genus and species	Family	No.	Resistance (kg)	
			Min.	Max.
<i>Ateles paniscus</i>				
<i>Alchorneopsis floribunda</i>	Euphorbiaceae	7	1.36	1.82
<i>Brosimum lactescens</i>	Moraceae	5	4.55	18.18
<i>Cordia sericicalyx</i>	Boraginaceae	10	11.36	18.18
<i>Eremoloma sagottiana</i>	Sapotaceae	1	2.73	2.73
<i>Guettarda aereana</i>	Rubiaceae	3	7.27	16.40
<i>Hyeronima laxiflora</i>	Euphorbiaceae	8	2.27	3.64
<i>Inga alba</i>	Leguminosae	5	13.64	19.09
<i>Pourouma guianensis</i>	Moraceae	5	1.82	7.27
<i>Pseudolmedia laevis</i>	Moraceae	3	66.82	148.18
<i>Rheedia macrophylla</i>	Guttiferae	1	47.73	47.73
<i>Sacoglottis cydonioides</i>	Humiriaceae	1	35.45	35.45
<i>Tetragastris altissima</i>	Burseraceae	3	9.55	13.64
<i>Viola melinonii</i>	Myristicaceae	13	9.09	22.73
Mean $\pm$ S.E.		65	17.09 $\pm$ 2.64	
Range			1.36	148.18
<i>Chiropotes satanas</i>				
<i>Achrouteria pomifera</i>	Sapotaceae	3	1.36	1.82
<i>Brosimum lactescens</i>	Moraceae	5	5.45	16.36
<i>Carapa procera</i>	Meliaceae	10	0.45	1.82
<i>Clarisia racemosa</i>	Moraceae	7	4.55	11.36
<i>Clusia grandiflora</i>	Guttiferae	4	1.36	2.73
<i>Ecclinusa guianensis</i>	Sapotaceae	12	1.36	5.91
<i>Helicostylis tomentosa</i>	Moraceae	3	2.27	3.64
<i>Lecythis corrugata</i>	Lecythidaceae	6	1.36	12.27
<i>Lecythis chartacea</i>	Lecythidaceae	1	2.27	2.27
<i>Licania majuscula</i>	Chrysobalanaceae	1	15.45	15.45
<i>Moutabea guianensis</i>	Polygalaceae	8	6.36	18.18
<i>Naucleopsis guianensis</i>	Moraceae	4	3.64	6.36
<i>Quassia simarouba</i>	Simaroubaceae	4	4.55	7.27
<i>Sterculia excelsa</i>	Sterculiaceae	2	12.27	19.55
<i>Strychnos</i> sp.	Loganiaceae	1	0.23	0.23
<i>Viola melinonii</i>	Myristicaceae	6	20.45	22.27
<i>Xylopia nitida</i>	Annonaceae	7	0.91	5.00
Unknown	Apocynaceae	1	8.64	8.64
Liana No. 2		1	3.64	3.64
Mean $\pm$ S.E.		86	7.16 $\pm$ 0.66	
Range			0.23	22.27



species (McKey et al., 1981), seed testa may be quite toxic (Gartlan et al., 1980; Waterman et al., 1980). Limited studies of *Chiropotes* digestive morphology and physiology do not provide convincing evidence for anatomical specialization of the gut (Fooden, 1964; Milton, 1984; Ayres, 1986). Adaptations to leaf eating in colobine primates (Davies et al., 1984) may facilitate seed eating especially when these contain secondary compounds. If toxicity of seeds increases with maturation, animals able to open unripe fruit may be eating the seed at its maximum stage of digestibility. Pitheciin monkeys seem to share this adaptation, although little is yet known of *Pithecia*.

We suggest that fruit hardness (resistance to puncturing the outer covering—pericarp or exocarp) is a major determinant in food choice between these two primate species. *Chiropotes* is known to be a seed predator (Ayres, 1981, 1986; Mittermeier and van Roosmalen, 1981; Johns and Ayres, 1987; van Roosmalen et al., 1981, 1988), whereas the sympatric *Ateles* is a seed disperser (Mittermeier, 1977; van Roosmalen, 1980). We have demonstrated a possible mechanism for this distinction by measuring fruit hardness. In *Chiropotes* the incisors and canine are specialized to puncture and open the hard pericarp of fruit to obtain otherwise inaccessible nutritious (and frequently soft) seeds. It seems probable that by opening hard unripe husks *Chiropotes* is able to obtain nutritious seeds with high water content and a low concentration of toxic compounds, whereas, when the exocarp ripens (softens), the seed loses water content, hardens, and develops higher levels of secondary compounds. This selective mechanism has been suggested to explain seed predation by *Cacajao* (Ayres, 1986). We plan to document these chemical changes in the next phase of this study. The bearded saki monkey may be said to specialize in "sclerocarpic harvesting" or the preparation and ingestion of hard fruit. Based on their dentition (Kay, 1981), mangabeys may also be sclerocarpic harvesters in contrast with sympatric guenons; and the aye-aye, which eats hard nuts of *Canarium madagascariensis*, may be one as well (Iwano and Iwakawa, 1988). Hardness, often correlated with fruit size (Janson, 1983), may be an indicator of differences in resource partitioning (Schoener, 1974). Thus some sympatric vertebrates (e.g., squirrels [Smith, 1971; Emmons, 1980], desert rodents [Reichman, 1977], molossid bats

[Whitaker and Mumford, 1978; Freeman, 1979], characoid fish [Goulding, 1980]) may partition food resources on the basis of food hardness. In the method presented here we advocate measuring resistance to puncturing of exocarp and pericarp and resistance to crushing of seeds. Both measurements are necessary for understanding the significance of fruit hardness in fruit choice and in partitioning of resources.

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